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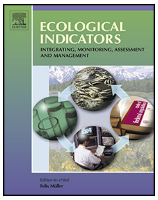

Functional diversity and trait–environment relationships of periphytic algae in subtropical floodplain lakes

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ABSTRACT

Assembly rules are ecological processes imposed on a regional species bank to establish the structure of communities and define diversity patterns regarding space and time. Here, we investigated the trait distribution of periphytic algae in floodplain lakes that are naturally under contrasting environmental pressures with and without flood pulse action (low and high water phases) and the relationship between functional traits and environmental variables at regional and local scales. We hypothesized that functional clustering will be related to the low water phase in local scale, based on environment filters, and functional overdispersion to the high water phase in regional scale. With respect to traits, we can expect that the flood pulse would favored the prevalence of nanoperiphyton, filamentous forms and loosely attached. For this, we conducted a two-year assessment of the structure and dynamic of periphytic algae communities regarding their functional traits in lakes belonging to two sub-basins in a subtropical floodplain (upper Paraná River floodplain). The samplings occurred during the high water phase in 2010 and 2011 and the low water phase in 2011. The functional diversity values of the communities were quantified and compared with the mean value of communities randomly generated using null models. The relationships between functional traits and environmental variables were examined using RLQ analysis. We have shown that the traits respond to abiotic factors, and they indicated overdispersion in high water phase, and higher functional diversity in most preserved environments with absence of the pulse. The flood pulse favored the prevalence of colonial life form, stalked, entangled and heterotrichous species. This study showed spatial and temporal differences in the limnological characteristics between the lakes caused by hydrological phase and local forces in different sub-basins and the importance mainly of assimilable nutrients in the evaluation of trait–environment relationships. The overdispersion result can be assigned to flood pulse, which promotes a higher probability of dispersion and colonization of new areas for rare species, disturbance and more heterogeneous habitats, allowing opportunities for resource partitioning and regeneration of different species strategies. Moreover, the higher periphytic algae functional diversity in preserved sites emphasizes the importance of understanding ecological patterns linked to environmental degradation, as well as of conservation initiatives, because variation in periphytic algal communities implies in changes in the trophic structure, dynamics and in the functioning of environments.

1. Introduction

Ecology has persisted in seeking patterns and generalizations for the structuring of species communities. One possible explanation is that there are a set of rules that can act on the formation and maintenance (assembly) of communities (Sobral and Cianciaruso, 2012). Assembly rules are ecological processes imposed on a regional

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species bank that determine the structure of communities and define the diversity patterns regarding space and time (Keddy, 1992). Environmental filters are assembly rules that represent the set of environmental conditions that restrict the establishment of species with unsuited trait values (Cornwell and Ackerly, 2009; Weiher et al., 2011). In this case, co-occurring species will have ecological strategies that are more similar than expected by chance (convergence in trait values or functional clustering) (Weiher and Keddy, 1995).

In contrast, another non-neutral process, the limiting similarity, determines that only low niche overlap would allow the coexistence of species on a local scale (Funk et al., 2008). This processes leads to trait divergence or overdispersion, where co-occurring species will have ecological strategies that are less similar than expected by chance, according to niche differentiation (a result from competition), occurring at a local scale (Laliberté et al., 2013). Trait overdispersion can also be the result of disturbance due to distinct regeneration strategies (Grime, 2006). Therefore, because those processes depend on the scale, environmental filters are expected to be more important on larger spatial scales, and the limiting similarity is expected to structure communities on lower scales (Webb et al., 2002).

Among aquatic organisms, periphytic algae are important for carbon fixation and oxygen production (Stevenson, 1996), and in floodplains, they are especially important in shallow environments for contributing to a greater part of primary productivity than phytoplankton (Robinson et al., 1997). Their ability to revel effects of pollutants and abiotic factors provided their use as bioindicators in many aquatic ecosystems (Montuelle et al., 2010; Lambert et al., 2015). However, little is known about the dynamic and response of their functional traits associated with environmental disturbances (Dunck et al., 2013). Limnological variables are important factors that affect periphytic algae structure reflected by trait values (Ferragut and Bicudo, 2010; Schneck and Melo, 2012; Dunck et al., 2015, 2016).

In floodplain systems the flood pulse is a typical disturbance and it is the main structuring force for these environments (Thomaz et al., 2007). These ecosystems have areas flooded by the overflow of rivers and lakes according to periodic fluctuations in the level of water (Goldsborough and Robinson, 1996; Junk and Wantzen, 2004), which are essential factors in the rearrangement of physical characteristics and consequently the organization and dynamic of aquatic ecosystems (Death, 2010). Over there, lakes belonging to a single sub-basin and permanently connected to the main river in the low water phase have similar limnological characteristics and can be different from other sub-basins (Taniguchi et al., 2004; Thomaz et al., 2007); during the high water phase, the flood pulse causes lakes of different sub-basins to have similar limnological characteristics (Roberto et al., 2009).

In this way, this type of disturbance can be traced at community level (Stenger-Kovács et al., 2013), as in the benthic algae community change, for example. It is thus necessary to understand the features that affect species in this ecossystems in order to implement effective conservation strategies, to mitigate biodiversity loss, assess ecological responses to natural and human disturbances, and detect changes in the structure and function of ecosystems (Magurran et al., 2010).

Functional diversity can be a tool to assess the differences in functional traits among communities (Di Battista et al., 2016); it estimates the differences among organisms directly through their functional characteristics (Díaz and Cabido, 2001). It is directly related to the functioning and maintenance of ecological processes because it is not only the number of species that influence community functioning but also their functional traits (Tilman, 2001; Petchey and Gaston, 2006). Therefore, the general expectation is that high values of functional diversity are associated with more efficient communities and the improved use of available resources (Sobral and Cianciaruso, 2012).

Here, we investigated the trait distribution of periphytic algae in floodplain lakes that are naturally under contrasting environmental pressures with and without flood pulse action (low and high water phases) and the relationship between functional traits and environmental variables at regional (all lakes together in high water phase) and local scales (lakes of different sub-basins are used separately in low water). The main goals were to compare the functional diversity between the high water and low water phase and between different sub-basins in the low water phase, to test the assembly rules and the trait–environment relationships in this context.

We tested the following hypotheses: the functional diversity of periphytic algae in a floodplain will be (i) lower than expected by chance (functional clustering) during the low water phase in lakes belonging to a single sub-basin (local scale) and (ii) higher (overdispersion) during the high water phase considering all lakes of different sub-basins together (regional scale).

Therefore, as predictions, we can expect that lakes belonging to the same sub-basin in the low water phase have similar limnological characteristics and that environmental filters will act as prevailing assembly rules in the structuring of periphytic algae communities, allowing only a narrow spectrum of traits to persist (functional clustering), and these traits will reflect the species ecological niche (minimum requirements to maintain a viable population). On the other hand, we can expect overdispersion in the high water phase considering all lakes as a result of niche diversification and the disturbance caused by the flood pulse, which provides more heterogeneous habitats and distinct species regeneration strategies. Heterogeneous habitats offer opportunities for resource partitioning and, consequently, allow greater permanence of species with different ecological traits (Bradford and Kastendick, 2010). With respect to traits, we can expect that the flood pulse would favored the prevalence of nanoperiphyton, filamentous forms and loosely attached when compared to the low water period (Dunck et al., 2015).

With these results we expect to be able to show in subtropical floodplain when and where the functional diversity of periphytic algae is higher and the main traits for each hydrological period and ecosystem type, important information for conservation initiatives and ecosystems processes as primary production.

2. Methods

2.1. Study area

We conducted this study in 2010 (high water phase-March) and 2011 (high water in March and low water in September) in six lakes belonging to the upper Paraná River floodplain. The lakes are permanently connected to the main river inserted in two sub-basins, the Ivinhema River sub-basin (Lake Patos – 22°49′33.66″S; 53°33′9.9″W, Lake Sumida – 22°46′54.78″S; 53°29′22.2″W, Lake Peroba – 22°54′30.3″S; 53°38′24.3″W) and the Paraná River sub-basin (Lake Bilé – 22°45′13.56″S; 53°17′9.48″W, Lake Leopoldo – 22°45′24″S; 53°16′7.98″W, Lake Pau Véio – 22°44′50.76″S; 53°15′11.16″W) (Fig. 1). The Ivinhema sub-basin is located in a protected area (Ivinhema River State Park) and has a higher richness of macrophytes and other aquatic communities, whereas the sampling sites in the Paraná sub-basin have poorer macrophyte richness (Thomaz et al., 2007).

All of the lakes are considered shallow (<3.0 m deep on average) with a general connection of 8 m in length. During the high water phase, the mean water level of the Paraná River is approximately 4.5 m, providing water flow to the Ivinhema River sub-basin as well

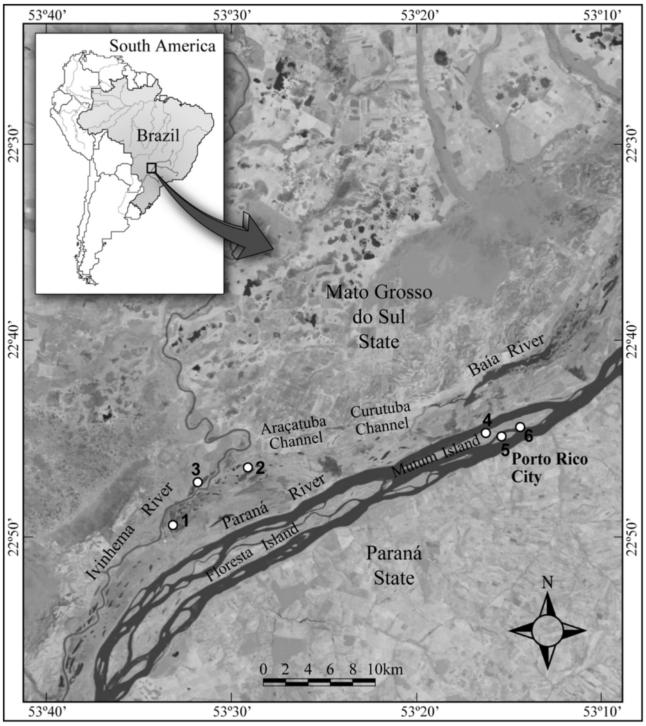

Fig. 1. Upper Paraná River floodplain (Lakes: 1 – Peroba, 2 – Patos, 3 – Sumida, 4 – Bilé, 5 – Leopoldo, 6 – Pau Veio; 1–3 Ivinhema River Sub-basin; 4–6 Paraná River Sub-basin).

as flooding the entire floodplain between the environments with connectivity from both sub-basins (Souza-Filho and Stevaux, 2004).

2.2. Sampling design

2.2.1. Environmental variables

We assessed the water levels of the Paraná River on a daily basis using a measure located at the advanced base of the Limnology, Ichthyology and Aquiculture Research Center (NUPELIA). We considered the amplitude (period in which the pulse remains above the overflow), magnitude (level height) and frequency (how many times the level increased during the phase) of the flood pulse according to Neiff (1990).

The sampling of abiotic variables (water temperature, dissolved oxygen, pH, water conductivity, transparence, turbidity, total solids, organic and inorganic solids, total alkalinity, phytoplankton chlorophyll-*a*, total nitrogen, nitrate, ammonium, total phosphorus and phosphate) was conducted on the subsurface of the limnetic zone of each lake concurrently with the abiotic variables. The abiotic variables were estimated according to a methodology presented by Roberto et al. (2009) and provided by the limnology laboratory of NUPELIA.

2.2.2. Periphytic algae

The macrophyte *Eichhornia azurea* (Sw.) Kunth was the substrate for periphytic algae, and it is the most abundant macrophyte in this floodplain and is present in all of the studied lakes. The periphytic algae community was obtained from two banks of *E. azurea* present in the coastal region of the lake in all samplings. Two submerged, mature petioles were collected (one per bank) at each lake, catching the sixth or seventh plant internode. These petioles were placed in 150-ml Wheaton bottles and kept on ice until the periphytic material was removed by a stainless steel blade wrapped in aluminum foil and by jets of distilled water (Algarte et al., 2014). The area scraped from the substrate (cm^2) was calculated by measuring the range (length and width) of each petiole. The periphytic material was removed from the substrate, fixed and preserved in 0.5% acetic acid lugol's iodine solution for further quantification.

For the periphytic biomass sampling (chlorophyll-*a*), we collected two petioles from two macrophyte banks of each lake. Chlorophyll-*a* values were estimated according to Golterman et al. (1978) with 90% acetone extraction and with the results expressed in μg/cm^2.

We used the Utermöhl method (1958) to quantify the algae, and the counting was conducted in random fields on an inverted microscope according to two criteria until at least 100 individuals of the most common species (cells, colonies and filaments) of each sample and a species – accumulation curve were reached (Ferragut and Bicudo, 2012). The density of periphytic species was estimated according to Ros (1979) with the results expressed as the number of individuals per area unit (ind/cm^2). We adopted the species classification system proposed by Round (1971).

2.2.3. Functional traits

The structure and dynamics of communities were also assessed regarding four functional traits of the algae distributed in 15 categories: life forms (non-motile unicellular, filamentous, flagellate or colonial), intensity of adherence to substrate (firmly or loosely attached – Sládecková and Sládecek, 1977), form of adherence (mobile, entangled, prostrate, stalked, or heterotrichous-differentiated basal cell – Biggs et al., 1998), and size class (nano: 0–20 μm, micro: 20–70 μm, meso: 70–120 μm, macro: >120 μm). These are the functional traits composing the functional matrix. These selected functional traits allow for the establishment of the periphytic algae on substrates, and they were analyzed directly through the individuals of each species.

2.3. Data analysis

We employed paired *t*-tests to assess the difference in the community structure (biomass, density, richness and functional diversity) between the studied hydrological cycles (high water phase was considered as the mean value between 2010 and 2011). The data were log-transformed whenever required to meet the assumptions of normality and homoscedasticity.

We used the principal components analysis (PCA) to assess the similarity among the lakes regarding the limnological variables during both hydrological cycles; the Broken-Stick criteria (Jackson, 1993) were applied to the retention of axes. All of the environmental variables, except pH, had been previously log(x)-transformed (Legendre and Legendre, 1998).

An RLQ analysis (Dolédec et al., 1996) was used to assess the relationship between the environmental variables and functional traits of periphytic algae among the sites considering hydrological cycles and sub-basin as factors. Hence, we conducted this analysis for the high water phase in 2011 and 2010 and for the two sub-basins in the low water phase. RLQ is based on the ordinations of three separate matrices (species abundance, environmental variables and species traits) and is an extension of co-inertia analysis that searches for a combination of traits and environmental variables of maximal co-variance, which is weighted by the abundances of species in the plots. We used permutation tests by the fourth-corner approach (Dray and Legendre, 2008) to test the relationship significance.

The functional traits matrix was standardized and transformed in a distance matrix through the mixed-variables coefficient of distance proposed by Pavoine et al. (2009). It provided the calculation of the functional diversity through mean pairwise distance (MPD), which considers the density of species in the estimate. This measure is considered basal (i.e., more sensitive to distant taxa) for calculating the pairwise distance between each species of a community (Webb, 2000). We estimated the high water functional diversity (2011 and 2010 together) and for the two sub-basins in low water. We employed paired *t*-tests to assess the difference between hydrological cycles and sub-basins (only for low water).

We used null models to test whether the species coexisting in the communities were lower or higher than expected by chance for the assessed hydrological cycles. The MPD values were compared with the mean value obtained from 1000 communities randomly generated using the independent swap algorithm, maintaining the richness and abundance of species in the null communities (Gotelli, 2000). Thus, we conducted this analysis for the high water phase in 2011 and 2010 and for the two sub-basins in the low water phase. For hypothesis (i), the regional species bank encompassed the communities of all species present in the lakes of a single sub-basin; for hypothesis (ii), all of the species present in the lakes of both sub-basins were included for the analysis of each year.

The extension of the MPD standardized effect, also known as the nearest relative index (NRI), was calculated as NRI = −1 (obs.value − rand.value)/sd, where 'obs.value' is the observed value corresponding to the MPD for the communities, 'rand.value' is the MPD mean value for the random communities, and 'sd' is the respective standard deviation for the 1000 values of the random communities. NRI values above zero indicate functional clustering (species functionally similar), while those below zero indicate functional overdispersion (species functionally dissimilar) (Gómez et al., 2010). A simple *t*-test was employed to test the hypotheses presented in this study, assessing whether the extension of the standardized effects (NRI) was, on average, significantly different from the expected random value (mean = 0) during the distinguished hydrological cycles and sub-basins in the low water phase. All of the analyses were performed using R software (R Development Core Team, 2014). Packages *ade4* (Chessel et al., 2004) and *picante* (Kembel et al., 2010) were used to construct the distance functional matrix and dendrogram; *picante* was used to calculate the functional diversity through mean pairwise distance and null models, *ade4* was used for the RLQ analysis, and *vegan* (Oksanen et al., 2013) was used for the PCA and *t*-tests.

3. Results

3.1. Taxonomic periphytic algae structure

Three hundred and twenty-four species of periphytic algae were found in the six studied lakes in the high water phase of 2010, 103 in the high water phase of 2011, and 104 in the low water phase of 2011. The Ivinhema River sub-basin had higher species richness (Table 1, Supporting Information). Thirty abundant species were found in 2010, 36 abundant species were found in the high water phase of 2011, and one dominant and 25 abundant species were found in the low water phase of 2011 (Table 1, Supporting Information). The dominant and abundant periphytic species in the samplings and their respective traits and abbreviations are shown in Table 1, Supporting Information.

The values for periphytic biomass varied from 94 to 10.000 $\mu g/cm^2$. In the high water phase, the biomass was four times higher than in the low water phase ($t = 4.21$, df = 34; $p = 0.001$), and the species richness was three times higher ($t = 3.40$, df = 22, $p = 0.002$). For species density, during the low water phase, the density was two times higher than during the high water phase ($t = -2.14$, df = 22, $p = 0.04$).

3.2. Environmental variables

Both sampling years experienced a similar magnitude of the water level of the Paraná River exceeding 4.5-m height when the high water phase flooded the entire plain (Fig. 2). The amplitude and frequency between the years were differentiated. Both years also had a similar amplitude considering the overflow level of the Paraná River during January and April. Considering the flood level of the entire lowland in 2010, the amplitude occurred between January and April but with oscillations (decrease) between February and March and between March and April. The year 2011 had a different amplitude, which occurred only between March and April (Fig. 2); however, the pulse frequency was higher in 2010 (Fig. 2).

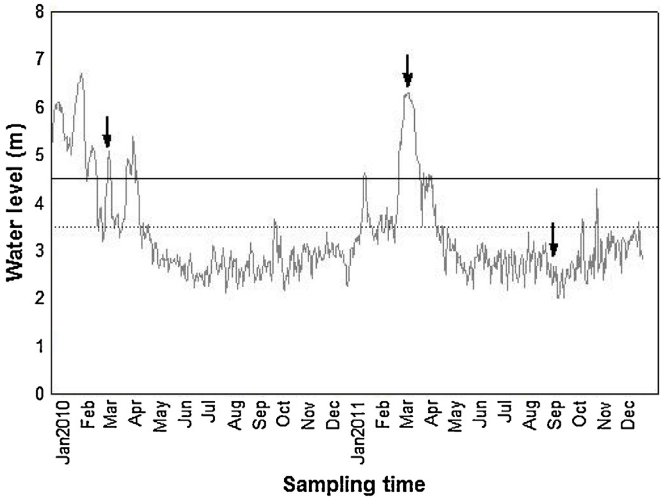

Fig. 2. Water level of the Paraná River between 2010 and 2011. Arrows indicate the sampling months; dashed line indicates overflow level of the Paraná River; continuous line indicates the flood level of the entire plain.

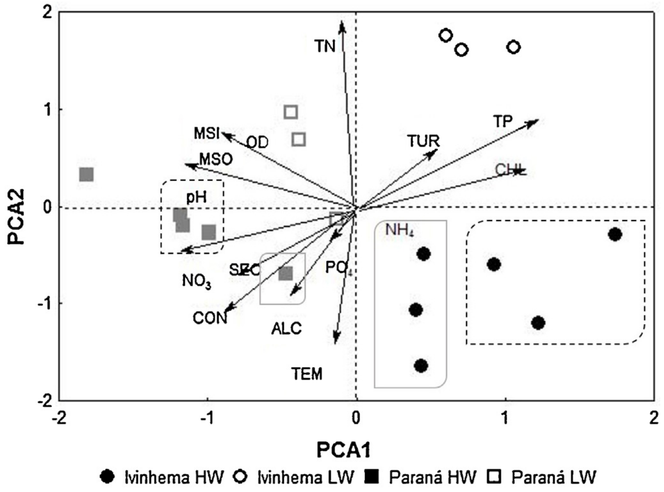

Fig. 3. Principal components analysis among lakes of different sub-basins during 2010 (HW) and 2011 (HW and LW). Group inside dashed line are samplings in 2010, and group inside gray line are samplings in 2011. (TEM – water temperature, DO – dissolved oxygen, pH, CON – water conductivity, SEC – transparence, TUR – turbidity, MSI – total inorganic solids, MSO – total organic solids, ALK – total alkalinity, CHL – chlorophyll-*a*, TN – total nitrogen, NO_3 – nitrate, NH_4 – ammonium, TP – total phosphorus, and PO_4 – phosphate).

The principal components analysis summarized 61% of the data variability in the first two axes, with eigenvalues of 5.75 and 4.10 for axis 1 and 2, respectively (Table 2, Supporting Information). The ordination pointed to similarity among the lakes of a single sub-basin for both assessed hydrological cycles (Fig. 3). The hydrological periods and sub-basins were separated by axis 1 and axis 2, respectively. The main variables correlated with the first axis was NO_3 ($r = -0.91$), pH ($r = -0.25$) and CHL ($r = 0.18$) (Table 2, Supporting Information). The main variables correlated with the second axis was pH ($r = 0.71$), turbidity ($r = 0.52$) and NH_4 ($r = -0.31$) (Table 2, Supporting Information). Both axis condensed a trophic gradient, separated by forms of assimilable nitrogen. Thus, in general, the lakes of the Ivinhema sub-basin presented higher levels of total phosphorus, turbidity and phytoplankton chlorophyll-*a* during the low water phase, whereas during the high water phase, the values were lower for pH, dissolved oxygen, total solids and total nitrogen. For the lakes of the Paraná sub-basin, the values were higher for conductivity, transparence and NO_3 associated with the high water phase, and lower values occurred for pH, total solids and total nitrogen during the low water phase (Fig. 3).

3.3. Trait–environment relationships

For the high water phase of 2010, the first two axes of the RLQ with eigenvalues of 5.4 and 0.10 for axes 1 and 2, respectively, accounted for 97% and 1% of the coinertia (Fig. 4(1)). The first axis was negatively correlated with all solids and NO_3 and positively correlated with total phosphorus, and the second axis was positively correlated with NH_4 (Fig. 4(1A)) (Table 3, Supporting Information). For traits, the first axis was correlated with the intensity of adherence to the substrate and the entangled form of adherence, and the second axis was correlated with the prostrate form of adherence (Fig. 4.1(1B)) (Table 3, Supporting Information). The permutation test showed ($p < 0.05$) that colonial life forms were correlated with dissolved oxygen, transparence and total solids (Fig. 5). Other correlations included filamentous life forms with total nitrogen, intensity of adherence to the substrate with dissolved oxygen and all solids, and stalked forms with dissolved oxygen, transparence and all solids (Fig. 5). Colonial life forms and stalked species were correlated with higher values of dissolved oxygen, transparence and total solids.

For the high water phase of 2011, the first two axes of the RLQ with eigenvalues of 0.71 and 0.56 for axis 1 and 2, respectively, accounted for 50% and 40% of the coinertia (Fig. 4.2) (Table 3, Supporting Information). The first axis was correlated with NH_4 and temperature, and the second axis was negatively correlated with total phosphorus and positively correlated with transparence (Fig. 4(2A)) (Table 3, Supporting Information). For traits, the first axis was correlated with the intensity of adherence to the substrate and the entangled form of adherence, and the second axis was correlated with filamentous life forms (Fig. 4(2B)). The permutation test showed that the entangled form of adherence was correlated with PO_4 and that the heterotrichous form of adherence was correlated with temperature, dissolved oxygen, turbidity and NO_3 (Fig. 5). Entangled species were correlated with higher values of PO_4, and heterotrichous forms were correlated with higher values of temperature, dissolved oxygen, turbidity and NO_3.

For the low water phase of 2011, the first two axes of the RLQ with eigenvalues of 6.3 and 0.13 for axis 1 and 2, respectively, accounted for 96.6% and 2% of the coinertia (Fig. 4(3)). The first axis was correlated with total phosphorus and conductivity, and the second axis was negatively correlated with total solids and total inorganic solids (Fig. 4(3A)) (Table 3, Supporting Information). For traits, the first axis was correlated with the intensity of adherence to the substrate and the entangled form of adherence, and the second axis was positively correlated with filamentous life forms and negatively correlated with the prostrate form of adherence (Fig. 4(3B)) (Table 3, Supporting Information). The permutation test showed that the entangled form of adherence was correlated with dissolved oxygen and the intensity of adherence to phytoplankton chlorophyll-*a* and NH_4 (Fig. 5). Entangled-type species were correlated with higher values of dissolved oxygen.

3.4. Functional diversity

We did not observe differences in the values of functional diversity during the two water phases ($t = 1.27$, df = 34, $p = 0.26$, Fig. 6). In the high water phase, the functional diversity was not different between 2011 and 2010 ($t = -0.75$, df = 22, $p = 0.45$). In the low water phase, the Ivinhema River sub-basin presented higher functional diversity ($t = -16.29$, df = 10, $p = 0.001$) (Fig. 6).

3.5. Null models

The results of the null models demonstrated that during the high water phase of 2011, the mean of NRI was below zero, indicating overdispersion (mean NRI = −0.54; $t = -2.36$, df = 11; $p = 0.037$); in 2010, the mean NRI did not differ from zero (mean NRI = −0.44; $t = -1.18$; df = 11; $p = 0.26$) (Fig. 7). During the low water phase, the mean NRI did not differ from zero for both sub-basins assessed (Paraná sub-basin: mean NRI = 0.08; $t = 0.09$; df = 5; $p = 0.93$; Ivinhema sub-basin: mean NRI = −0.33; $t = -0.78$; df = 5, $p = 0.47$) (Fig. 7).

4. Discussion

We have shown that periphytic algal functional structure was different in different sub-basin and under distinct hydrological periods. As we predicted, the traits respond to abiotic factors, and they indicated overdispersion in high water phase (2011), with higher functional diversity in most preserved environments in the low water phase. For the high water phase of 2010 the presence of colonial life form and stalked species was related to high values of dissolved oxygen, transparence and total solids. In 2011 the presence of entangled species was related to high values of PO_4 and heterotrichous form with high values of temperature, dissolved oxygen, turbidity and NO_3. In low water phase, the presence of entangled-type species was related to high values of dissolved oxygen. Unlike our predictions, flood pulse favored the prevalence of colonial life form, stalked, entangled and heterotrichous species.

In 2010 and 2011 the Upper Paraná River had two typical flood years when all of the floodplains were flooded; therefore, both years presented a great magnitude of pulse. However, the greatest frequency and amplitudes in 2010 are important characteristics in causing distinguished alterations in the habitats between the two years, changing the physical and chemical characteristics of the lakes, which modifies the stability of the system as well as the structuring and substitution of the community species (Neiff, 1990).

During the low water phase, the lakes belonging to the Ivinhema sub-basin presented higher levels of total phosphorus, turbidity and phytoplanktonic biomass, while the Paraná sub-basin had higher values of pH, total solids and total nitrogen. During the high water phase, the Ivinhema sub-basin had lower values of pH, dissolved oxygen, total solids and total nitrogen, while the Paraná sub-basin had lower values of pH, total solids and total nitrogen. These results highlight the spatial and temporal differences in limnological characteristics between the lakes caused by the hydrological phase and local forces in different sub-basins (Thomaz et al., 2007).

The analysis of taxonomic periphytic algae structure showed that regarding the species richness and biomass of this community, higher values were associated with the high water phase and the lakes belonging to the Ivinhema sub-basin; during this period, the flood and the great connectivity favored a greater dispersion of propagules and organisms among the environments. Other studies had also observed the same pattern for the richness in this floodplain (Fonseca and Rodrigues, 2005; Algarte et al., 2006; Algarte et

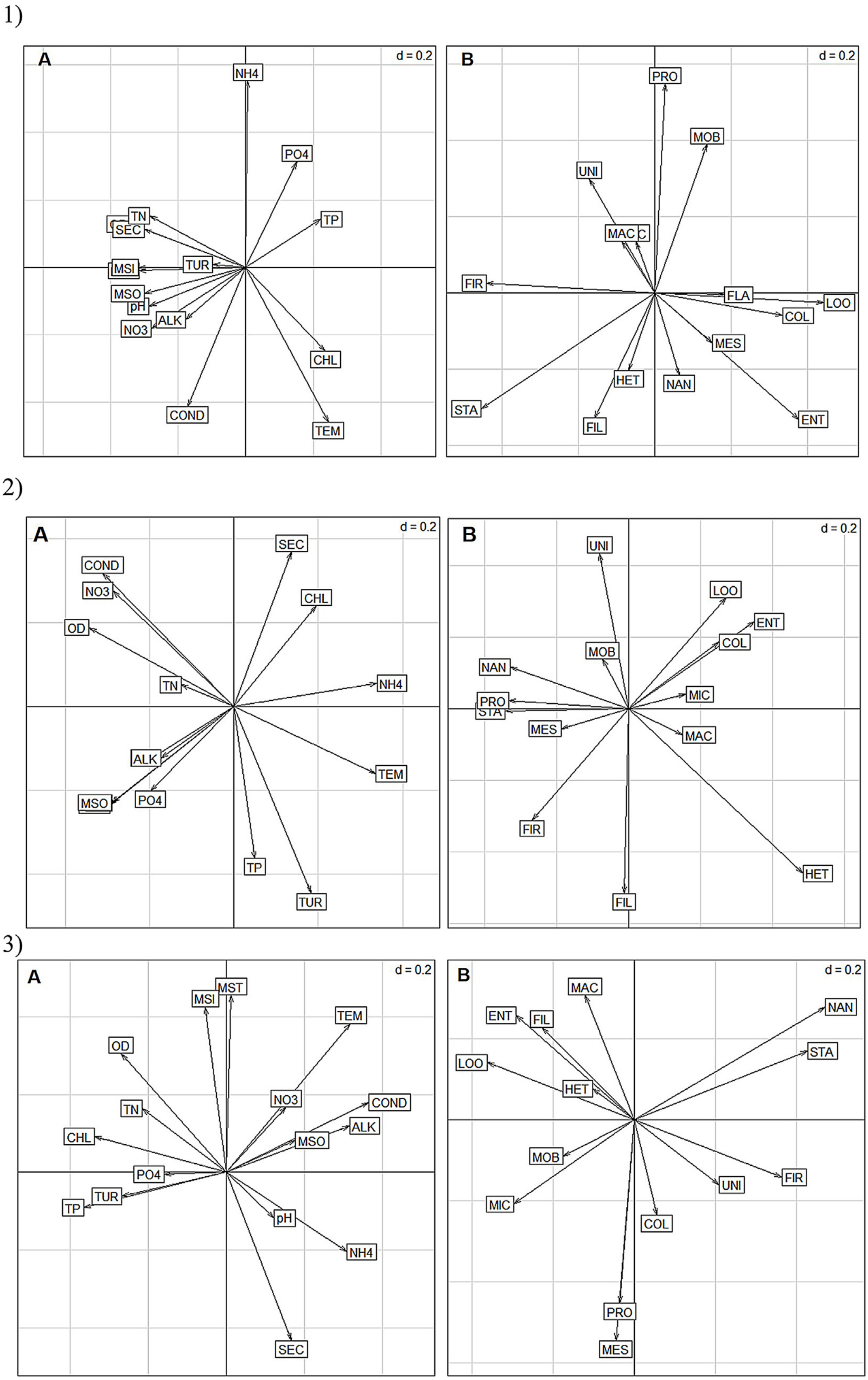

Fig. 4. Ordination of RLQ scores of environmental variables (A) and functional traits (B) of periphytic algae in lakes in high water phase of 2010 (1), high water phase of 2011 (2) and low water phase of 2011 (3) (TEM – water temperature, OD – dissolved oxygen, pH, COND – water conductivity, SEC – transparence, TUR – turbidity, MSI – total inorganic solids, MSO – total organic solids, ALK – total alkalinity, CHL – chlorophyll-*a*, TN – total nitrogen, NO_3 – nitrate, NH_4 – ammonium, TP – total phosphorus, PO_4 – phosphate, UNI – non-motile unicellular, FIL – filamentous, FLA – flagellate, COL – colonial, FIR – firmly attached, LOO – loosely attached, MOB – mobile, ENT – entangled, PRO – prostrate, STA – stalked, HET – heterotrichous, NAN – nano, MIC – micro, MES – meso, MAC – macro).

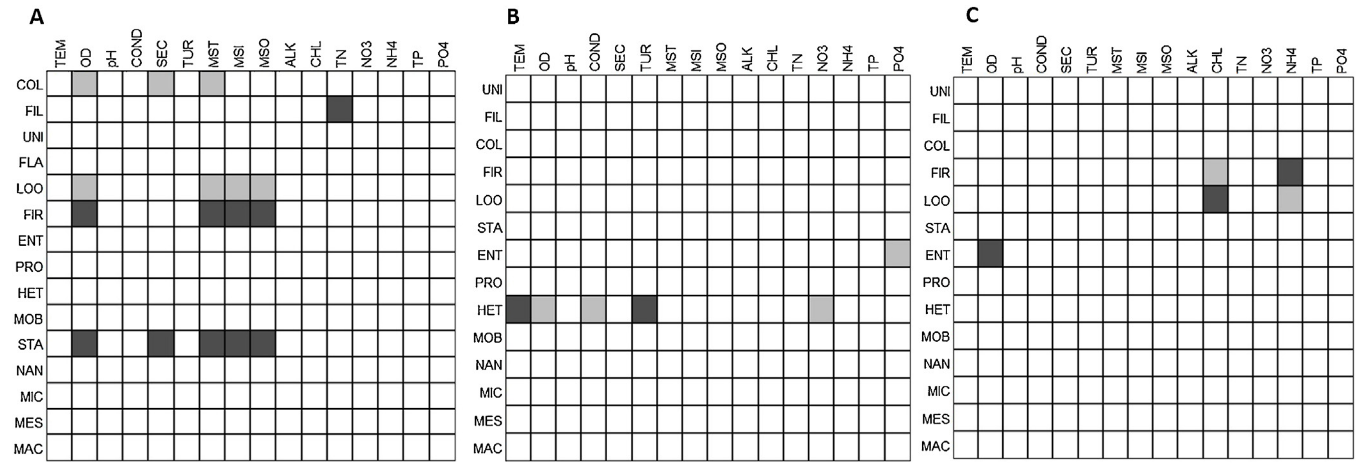

Fig. 5. Permutation tests by Fourth-corner approach based in RLQ analysis. Dark gray cells shows $p < 0.05$ and gray cells $p < 0.01$ (A – high water phase of 2010, B – high water phase of 2011, C – low water phase of 2011, TEM – water temperature, OD – dissolved oxygen, pH, COND – water conductivity, SEC – transparence, TUR – turbidity, MSI – total inorganic solids, MSO – total organic solids, ALK – total alkalinity, CHL – chlorophyll-*a*, TN – total nitrogen, NO_3 – nitrate, NH_4 – ammonium, TP – total phosphorus, PO_4 – phosphate, B-UNI – non-motile unicellular, FIL – filamentous, FLA – flagellate, COL – colonial, FIR – firmly attached, LOO – loosely attached, MOB – mobile, ENT – entangled, PRO – prostrate, STA – stalked, HET – heterotrichous, NAN – nano, MIC – micro, MES – meso, MAC – macro).

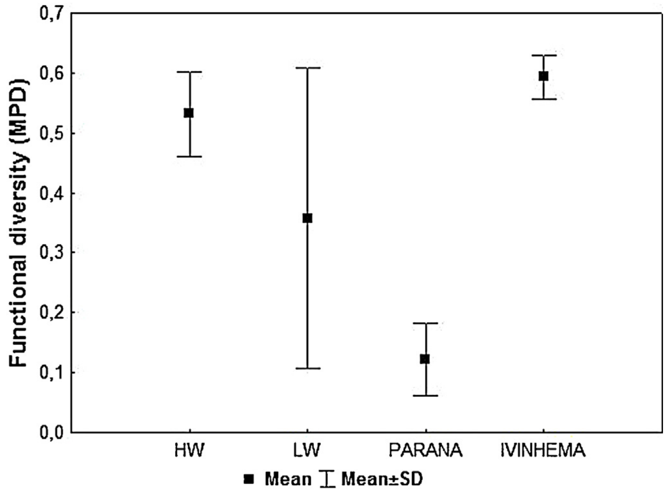

Fig. 6. Functional diversity (mean ± standard deviation) of periphytic algae among the sub-basins during 2010 and 2011 (HW – high water period, LW – low water period, IVINHEMA – Ivinhema sub-basin in low water 2011, PARANÁ – Paraná sub-basin in low water in 2011).

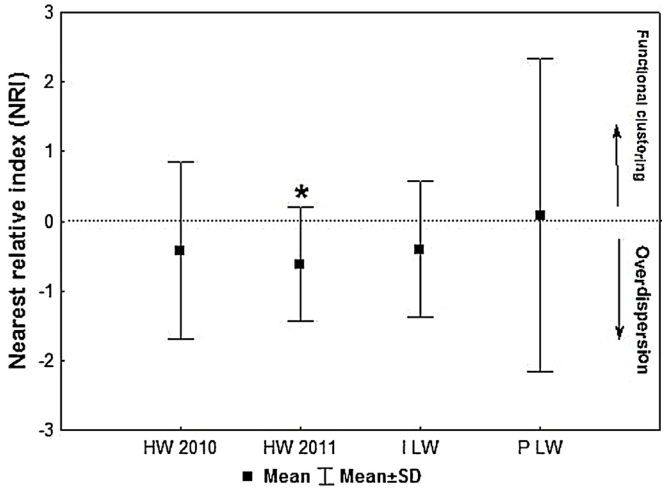

Fig. 7. Extension (mean ± standard deviation) of the MPD standardized effects (NRI) (*nearest relative index*-NRI) between 2010 and 2011. Dashed line represents separation between functional clustering and overdispersion. Asterisk (*) above bars indicate values significantly different than expected by chance (Tukey's test, $p < 0.05$) (HW – high water phase, LW – low water phase, I – Ivinhema sub-basin in low water of 2011, P – Paraná sub-basin in low water of 2011).

al., 2009). In turn, the higher density values during the low water phase can be associated with the decrease in physical disturbance and the high levels of total phosphorus. The ability of benthic algae to grow and become established is a set of a complex series of interactions between hydrological, water quality, and biotic factors, and low biomass can occur because of disturbances such as floods or a streambed dominated by continuously unstable bed sediments (Biggs, 1996), as in our high water phase, while in the low water phase, there is a decrease in physical disturbance.

The analysis of the trait–environment relationships demonstrated differences concerning the hydrological cycles. Such alterations corroborate the conclusions by Passy (2007), Lange et al. (2011), Rimet and Bouchez (2011), Schneck and Melo (2012), Law et al. (2014) and Dunck et al. (2015) demonstrating changes in the functional traits and life forms due to environmental changes. Colonial life form and stalked species were correlated with dissolved oxygen, transparence and total solids (high water phase of 2010). Colonial life forms are widespread in the periphyton developing in aquatic systems, where the current velocity is not only the major mechanical force. By affecting the ion and nutrient transport within the benthic mat (Stevenson and Glover, 1993), the current also has a complex physicochemical effect on the periphyton (Stevenson, 1996). Studies have indicated the predominance of stalked species when resources are not so restricting (Lange et al., 2011). Furthermore, adhesion favors greater access to the nutrients of the water column and their location at superior layers of the periphyton matrix (Passy, 2007) and makes them more susceptible due to the action of physical factors when removing the biofilm. Filamentous species were correlated with total nitrogen. Filamentous species are favored by vertical growth, which allows for greater access to light and nutrients from the water column (Margalef, 1983). Thus, for these traits, dissolved oxygen, transparence, total solids and total nitrogen appear to be the limiting environment variables.

In contrast, heterotrichous form with temperature, dissolved oxygen, turbidity and NO_3, and the entangled species with PO_4 (high water phase of 2011). Ferragut and Bicudo (2010) noted that adherence forms were mainly affected by the increase in nutrient availability in the experimental study. In 2011, the entangled and heterotrichous adherence forms appeared to be limited by PO_4 and NO_3, respectively. Entangled-type species (metaphytic) can tangle among the stalks of many species to become resistant to disturbance (Tuji, 2000) and remain more superficially in the periphyton. Heterotrichous species have stronger adherence force and can remain on a substrate before physical disturbance (Biggs et al., 1998). On the other hand, in low water phase the entangled-type species were correlated with dissolved oxygen. These results highlight the importance mainly of nutrients in the structuring of periphytic algae traits as noted by many studies (Bourassa and Cattaneo, 2000; Ferragut and Bicudo, 2010; Larson and Passy, 2012) and the importance of the hydrological cycle (Fonseca and Rodrigues, 2005; Algarte et al., 2014).

The functional diversity results indicated that there were not differences between the two water phases, and in the low water phase, the Ivinhema sub-basin presented the higher functional diversity. Between water phases, it was intuitive to think that the high water phase would have higher functional diversity caused by the flood, which favors a greater dispersion of propagules and organisms among the environments and a greater availability of temporary habitat and the variety of niche during this hydrological period (Gopal, 1994). This same water phase had higher periphytic algae biomass, and with these results, we can say that biomass was not correlated with functional diversity. An important advance in this research line should assess the primary productivity of these communities and relate it to biomass and functional diversity, perhaps in a short time series.

The higher functional diversity in the Ivinhema sub-basin can be attributed to the difference in ecosystem integrity between these two sub-basins. The Ivinhema sub-basin is a preserved ecosystem showing pristine conditions (Rodrigues et al., 2015) that can promote a greater availability of habitat and a variety of niches for periphytic algae species, since it has a higher richness of macrophytes and other aquatic communities than Paraná sub-basin (Thomaz et al., 2007). This greater heterogeneity is related to more complex habitats, and complex habitats offer better partitioning of resources and can support more ecologically different species together (Schoener, 1974). And, considering the species diversity this pattern also has been observed, with the Paraná sub-basin environments with lower species diversity over time compared with Ivinhema environments, manly due environmental degradation (Rodrigues et al., 2015).

The null model results did not indicate an effect of environmental filters in the low water phase on the functional diversity of periphytic algae. On the other hand, overdispersion occurred in the high water phase (2011). The flood pulse is known to be an important physical driving force in explaining the patterns of aquatic assemblages in tropical floodplains (Boschilia et al., 2008). Floods promote more heterogeneous habitats, which consequently offer opportunities for resource partitioning and allow for greater permanence of species with different ecological traits (Bradford and Kastendick, 2010). Nevertheless, the high water phase also involves a higher probability of dispersion and colonization of new areas for rare species and the regeneration of different strategies depending on the flood disturbance. All of these factors together provide niche differentiation and support the establishment of more species with different traits (Herben and Goldberg, 2014). As expected, the high water phase resulted in communities with greater-than-random variation in trait values (Weiher and Keddy, 1995). Weiher and Keddy (1995) also note that with the increase in scale, such as our results considering two sub-basins in the high water phase, models of functional overdispersion occur first by following neutral processes and later tending to change to functional clustering, where environmental filters are the major structuring factor.

Considering a floodplain, we can emphasize that dispersal is an important factor in structuring the functional diversity of periphytic algae (Algarte et al., 2014) compared with the effect of the limiting similarity for being strongly facilitated during the high water phase with greater connectivity among the environments. Weiher et al. (2011) suggest that dispersal, niche and trait interdependence have relatively equal effects on functional assembly. Therefore, we can emphasize that the functional traits associated with the ability of dispersion should be considered (Prinzing et al., 2008) when analyzing the functional diversity of periphytic algae in floodplains.

In summary, our study highlights the spatial and temporal differences in limnological characteristics between the lakes caused by the hydrological phase and local forces in different sub-basins and the importance mainly of assimilable nutrients and the hydrological cycle in the evaluation of trait–environment relationships. The finding that community assembly was deterministic (non-neutral processes) with respect to traits indicating overdispersion in the high water phase demonstrated that the flooding promotes a higher probability of dispersion and colonization of new areas for rare species, disturbance and more heterogeneous habitats, enabling opportunities for resource partitioning and the regeneration of different species strategies, making this hydrological phase essential for the maintenance of these communities.

Moreover, the higher periphytic algae functional diversity in preserved sites (Ivinhema sub-basin) emphasizes the importance of understanding ecological patterns linked to environmental degradation, as well as of conservation initiatives. Variation in periphytic algal communities implies in changes in the trophic structure, dynamics and in the functioning of environments, because they are primary producers and they affect the growth, development, survival and reproduction of many organisms.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2016.02.060.

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